LONG ENVIRONMENT CHANGE IN THE FOREST STEPPE HABITAT OF THE GREAT HUNGARIAN PLAIN BASED ON PALEOECOLOGICAL DATA

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Introduction

A treeline is a boundary used for marking the edge of the habitat at which trees are capable of growing. In ecology an upper and lower treeline is generally highlighted with an additional transitional zone (ecotone) found between the referred boundary and the adjacent open vegetation areas. The emergence of transitionary zones between woodlands and grasslans (ecotone) is generally controlled by the availability of water/humidity as a limiting factor. This boundary is mostly referred to as lower or dry treeline in contrast to the alpine and arctic treelines. The area of the Carpathian Basin is highly unique from the point that both treeline zones are present. Within the belt of the Alps, Dinarides and the Capathians, embracing the basin itself, an ecotone related to the upper or alpine treeline developed roughly at an elevation of 1700–2300 meter due to mainly temperature constraints. Conversely, climatic and geomorphological endowments within the heart of the basin favored the emergence of a forest-steppe ecotone along a dry or lower treeline. The area of the Great Hungarian Plains hosts a lower or dry treeline with an unusually wide ecotone, where the actual steppe zone is not uniform (MOLNÁR et al., 2007) but rather constitutes a mosaic of more or less isolated grassland patches (SÜMEGI, 2011). Nevertheless, it must be kept in mind that the modern landscape is highly transformed due to intensive human activities present during the past 8000 years. So the original vegetation must have been only partially preserved. One must turn to various environmental historical archives including pollen, charcoal, phytolith and plant macrofossil data, as well as terrestrial mollusks if he or she wants to reconstruct shifts in the lower and upper treeline for the late ice age and the Holocene.

Modern woodland-grassland ecotone in the Carpathian Basin and controversies around definitions

In general three prevailing theories are available in the literature for the development of the so-called Pannonian forest-steppe. According to the first, the forest-steppe found in the heart of the Carpathian Basin is an interim continuation of the Eastern European forest-steppe belt, which emerged as a result of the extreme drought literally exterminating arboreal elements in the area (KERNER, 1863). This concept, held for over 150 years with only slight modifications (SOÓ, 1926; BORHIDI, 1961), considers the modern Pannonian forest-steppe as an independent westernmost island-like fragment of the European continental oak forest-steppe, which emerged at the transitionary climatic zone of closed woodlands and grasslands separated from the main belt by the ranges of the Carpathian Mts (LAVRENKO, 1980; LAVRENKO –

KARAMYSEVA, 1991). This concept regards the woodland-grassland ecotone in the basin as local manifestation of the climate-zonal vegetation belt stretching roughly 8000 kms from the heart of Europe to the Far East (VARGA et al., 2000). One of the most significant pitfalls of this theory is that macro-climate conditions generally characteristic of the steppe belt (LAVRENKO – KARAMYSEVA, 1991: p. 254) have never fully developed and stabilized in the Carpathian Basin during the Quaternary. Winters are not cold and summers are not dry enough in the referred study area to enable the long-term macro-climatic sustainment of such vegetation, as it is clearly seen in the map of the western, European margin of the Eurasian steppe belt as well. Thus proving the macroclimatic nature of the ecotone in the area of the Carpathian Basin between the belt of European woodland and Eurasian steppe is quite ambiguous.

Conversely, in order to better highlight the climatic background of the woodland-grassland ecotone system, which is present in the heart of the Carpathian Basin, the vegetation classification system of Holdridge (HOLDRIDGE, 1947) is better suited than the climate classification system of Köppen (SZELEPCSÉNYI et al., 2009). According to the Holdridge classification (Fig.1a,b), the major part of the basin is put to the transitional category found between those of cold, temperate grasslands, cold, temperate humid woodlands and warm, temperate dry woodlands, where the first (steppe) and the last categories (dry woodland) also turn up climatically in the form of scattered patches. This grassy area forming an ecotone between the actual grasslands and dry and humid woodlands corresponds to the Pannonian forest-steppe vegetation of the Great Hungarian Plains (SZELEPCSÉNYI, 2012).

The second one considers so-called edaphic factors (soil, geomorphology) being responsible primarily for the emergence of forest-steppe ecotone in the basin (ZÓLYOMI, 1958, 1987). According to this concept, the heart of the Carpathian Basin is considered to be a part of the woodland belt from the point of climate zonal classification. Thus the opening of closed woodland and the appearance of parkland and grassland patches must be attributed to local abiotic ecological factors. Some of these factors might have direct influence on vegetation development, such as the interaction of soils and groundwater in relation to local geomorphology (shallow soils, alkaline and calcareous sandy soils and low groundwater table). Edaphic forest-steppes generally emerge along the northern margin of the steppe belt, where favorable soil, morphology and hydrological conditions enable the emergence of woodlands patches. The opposite may also be true when unfavorable local hydrology, soil, and morphology brings about the opening up of closed woodland creating isolated grassland patches. Unfortunately, these edaphic factors cannot explain the collective presence of phytogeographically, climatically exclusive Continental and Sub-mediterranean forest-steppe elements in the Carpathian Basin (ZÓLYOMI, 1957; BORHIDI, 1956).

The third explanation claims human activities being responsible for the opening of the original woodland vegetation and the emergence of a Pannonian forest-steppe (BERNÁTSKY, 1914; RAPAICS, 1918). The first such disturbances are linked to the first farming cultures settling in the basin. Initial clearings gradually expanded as human activities intensified parallel with cyclical population growth. These activities thus contributed to the sustainment of a highly variegated, mosaic-like forest-steppe vegetation in the Great Hungarian Plains as early as prehistoric times. This concept is still widely acknowledged despite the contrasting results of recent paleoecological investigations which pointed to the emergence of natural steppe-forest-steppe communities here, covering several hundred square kms, as early as the terminal part of the last ice age and the opening of the Holocene (SÜMEGI, 2005). Similarly, the application of paleoecological methods including archeobotany and archeozoology was also negligible. The lack of reliable, quantitative data regarding the number of sites, the size of the population further hampered the correct answering of such hypothetical questions. Nevertheless, it is important to note, that it was this period when the first major war (WW1) restricted wide-scale scientific studies on the one hand. On the other hand, the first negative outcomes of the 19th century river regulations also began to turn up during this period fueling notions of devastating human activities on local ecosystems. The general lack of archeological data on local cultures hampered the deduction of correct postulations regarding the influence of humans on the environment. Thus often the findings of similar scope studies related to distant high cultures of Egypt, Mesopotamia and the Near East were erroneously adapted to the area of the Carpathian Basin as well. These initial postulations were so influential that they still influence the acknowledgement of the results of new archeological, paleobotanical and archeozoological studies using correctly obtained hard data in Hungarian environmental historical research.

The environmental history of the Great Hungarian Plains

The original ecosystem of the Great Hungarian Plains hosting the Pannonian forest-steppes was fundamentally altered during the middle of the 19th century as a result of human intervention into probably the most important ecological component of the landscape: the fluvial system of the Tisza and its watershed. As a result of the extensive river regulation and flood protection measures, a 4000 km-long dike system and a canal system of 22.000 km was established. As a result of these activities in addition to the artificial cut of selected meanders the complete hydrological system of the Great Hungarian Plain was transformed seriously affecting not only the landscape and the vegetation but the trajectory of regional and local climate as well. The active floodplain originally covering an area of ca 30.000 km^2 was reduced to a mere 3000 km^2. The dried up floodplain areas were transformed into arable and pasturelands. The major part of the gallery forests fringing the riverbed was logged down to reduce costs of the regulation measures. Not only the majority of the original floodplain vegetation was destroyed, but by modifying the natural hydrological link between the river and the floodplain the hydrological system transporting the excess waters of the surrounding mountains coming from the precipitation was fundamentally altered as well during the past 160 years. As only a single cartographic map sequence, prepared on a non-geometric basis, is available for the landscape of the Great Hungarian Plains preceding the 19th century river regulations (Map of the 1st Austrian Military Survey, 1782), the only way to track the vegetation history including those of forest-steppes is to turn to environmental historical and paleoecological records. In order to highlight the vegetation history of the Carpathian Basin for the period from the terminal part of the last ice age, results of extensive paleoecological investigations implemented on 20 selected loess/paleosol sequences, including charcoal analysis, mollusk analysis (SÜMEGI, 2005; SÜMEGI – KROLOPP, 2002; HUPUCZI – SÜMEGI, 2010), and phytolith analysis (PERSAITS – SÜMEGI, 2011) has been adopted. In addition, findings of similar type of studies (palynology, mollusk and plant macrofossil analyses) deriving from radiocarbon-dated, undisturbed core sequences of 20 catchment basins have been utilized. These data have been complemented by records of mollusk, pollen and phytolith analysis implemented on nearby archeological sites. A combination of data enabled us to track not only temporal but spatial differences in the trajectory of vegetation evolution.

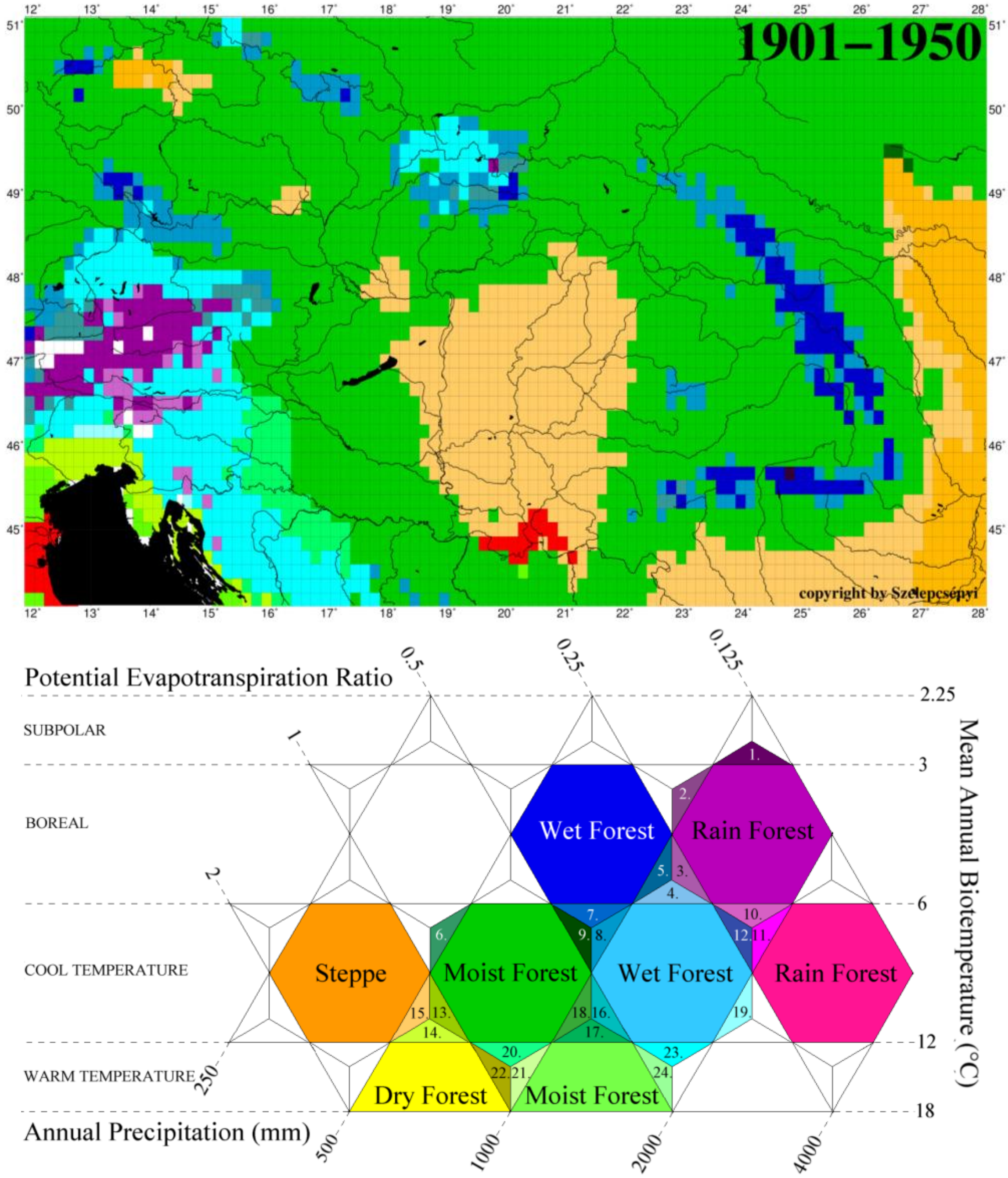

*Fig.1. Possible climato-vegetation zones of the Carpathian Basin based on Holdridge type bioclimatic classification method (*SZELEPCSÉNYI*, 2012)*

*1. ábra. A Kárpát – medence éghajlatilag lehetséges növényzeti övezetei Holdridge bioklimatikus módszere alapján (*SZELEPCSÉNYI*, 2012)*

Paleoenvironmental development during last ice age

Based on our findings, two major paleoenvironmental regions could have been identified within the area of the Carpathian Basin, which were characterized by fundamentally different endowments and developmental histories durin g the course of cyclical coolings characterized by loess formation and intervening warm-ups resulting in the temporary cessation of dust accumulation (SÜMEGI, 2005).The resolution of our records enabled us to capture the environmental history of the northern region for the past 70 kys (Fig. 2a). The warm-up periods were all characterized by the general spread of spruce. Within the emerging open parkland type spruce woodland ecosystems (WILLIS et al., 2000), sheltered spots hosted stands of Scots pine, and hornbeam (RUDNER – SÜMEGI, 2001), while the higher areas were populated by stands of Swiss pine and larch. Water bank areas hosted populations of willow, hairy birch and green alder. Moving towards the centre of the Great Hungarian Plains arboreal elements become less frequent components of the vegetation yielding a special tree-steppe ecosystem characterized by the dominance of non-arboreal elements even during the warm-ups as well. At the same time, the inner, drier areas, characterized by a prevalence of grassland type vegetation also hosted scattered stands of Scots pine, juniper, alder, birch and willow (SÜMEGI et al., 2005), restricted mainly to the banks of watercourses. One of the driest areas of the Great Hungarian Plains, the Hortobágy, which is extensive alkaline grassland today, was hosting some alkaline elements *(Artemisia maritima, Sueda)* even during this early period as well. However, the banks of minor watercourses also hosted a loose canopy gallery forest composed of Scots pine, alder and birch here as well.

The same warm-up period was characterized by similar tree steppe vegetation in the region south of the centre of the Great Hungarian Plain (Fig. 2b). However, this similarity was true for the structure of the vegetation alone. The taxonomic composition of the flora and the fauna was fundamentally different. The dry loess plateaus of the southern part of the Carpathian Basin hosted a mix of arboreal elements (Scots pine, birch and fir) during the referred warm-ups (RUDNER – SÜMEGI, 2001; SÜMEGI, 2005). However, as shown by data from charcoal and phytolith analysis the presence of arboreal elements was spatially highly dissected and highly subordinate compared to that of non-arboreal forms. Conversely, areas with an ideal hydrology and higher groundwater table, like along the banks of rivers and watercourses, lush mixed gallery forests emerged characterized by a 70–80% closed canopy. Thus the dry tree steppe vegetation of the Great Hungarian Plains studded by scattered stands of trees was highly dissected at the regional or meso level by closed-canopy gallery forests along the riverbanks during the ice age. Furthermore, in accordance with the local morphological, geological and hydrological endowments the emergence of full hydro series from the riverbed up to the elevated dry plateaus of the floodplain could have been attested.

An increase in dry grassland areas was accompanied by the spread of xerophylous, grassland mollusk taxa. It was this zone, where the representatives of the character species of modern Pannonian steppe/forest-steppe areas *Granaria frumentum* first turn up in the southern parts of the basin. The accessory fauna is very similar in composition to that of the modern Pannonian forest-steppe areas. Accordingly, the warmer periods of the terminal Pleistocene must have created ideal conditions for the spread of this type of mollusk fauna in the southern parts of the Carpathian Basin. On the basis of the paleodistribution of the mollusk species *Granaria frumentum*, the area of the Pannonian steppe/forest-steppe belt must have expanded as far north as the heart of the basin during the interstadials (SÜMEGI – KROLOPP, 2002). However, this zone managed to conquer the foothills of the Carpathian Mts. during the last interglacial (SÜMEGI – KROLOPP, 2002).

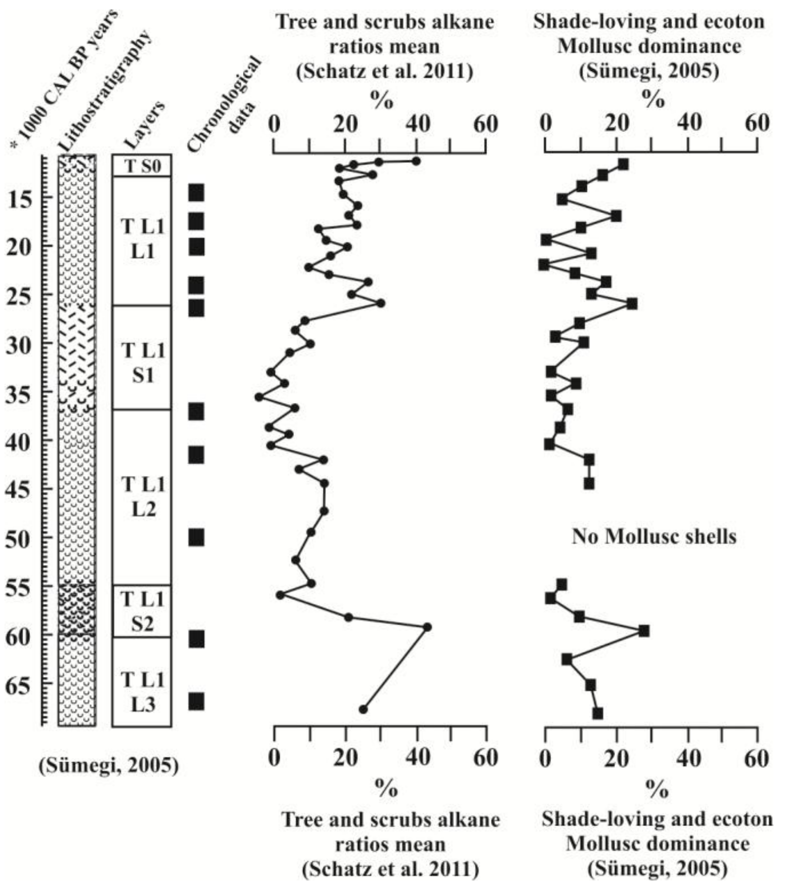

Fig.2a. Changes observed in the composition of plant alkanes and the terrestrial mollusk fauna in the area of the Northern Great Hungarian Plains for the past 70 kys

2a. ábra. A növényi alkánok és a Mollusca fauna összetételének változása az elmúlt 70 ezer évben az Észak-Alföldön)

T S0 = Tokaj, modern soil, T L1L1 = Late Pleniglacial Loess layer, T L1S1 = Middle Pleniglacial Paleosol layer, T L1L2 = Middle Pleniglacial Loess layer, T1 L1S2 = Early Pleniglacial Paleosol layer, T L1L3 = Early Pleniglacial Loess layer

T S0 = Tokaj, recens talaj, T L1L1 = késő-pleniglaciális lösz, T L1S1 = középső-pleniglaciális paleotalaj, T L1L2 = középső-pleniglaciális lösz, T1 L1S2 = kora-pleniglaciális paleotalaj, T L1L3 = kora-pleniglaciális lösz

During the LGM, vegetation development in the northern part of the Carpathian Basin followed a clear and characteristic path. Namely, the prevalence of a treeless steppe was interrupted by rapid phases of forest expansion lasting for several centuries twice. This is seen in the trajectories of open parkland boreal pine forest expansion and the accompanying woodland element of the Carpathian spindle snail *(Vestiga turgida)*. These forest expansion periods were first identified on the basis of shifts observable in the composition of the mollusk fauna (SÜMEGI – KROLOPP, 2002; SÜMEGI, 2005), and later corroborated by pollen (WILLIS et al., 2000), charcoal (RUDNER – SÜMEGI, 2001) and plant alkane data (SCHATZ et al., 2010). The inferred LGM mosaic of cold steppe studded by spots of tundra and woodland patches could have been correlated with the modern landscape of the altai Mts and its foothill areas on the basis of the composition of the accessory mollusk fauna (SÜMEGI, 2005; HORSAK et al., 2010, MENG – HOFFMANN, 2009). Thus the modern alpine boreal forest-steppe areas of Southern Siberia serve as an ideal analogy for the ice age vegetation of the Carpathian Basin (SÜMEGI, 1996, 2005; SÜMEGI et al., 1999).

The temporal resolution of our records enabled us to continuously capture vegetation changes in the southern parts of the Carpathian Basin for the past 140 kys; i.e. from ca. the last interglacial (ZECH et al., 2010). The presence of a steppe/forest-steppe vegetation hosting the marker taxon *Granaria frumentum* could have been attested in the area of the Great Hungarian Plains and the marginal part of the Carpathians as early as 110–130 kys. In contrast the foothills hosted a closed woodland vegetation. Nevertheless, besides the warm-ups during the terminal part of the ice age referred earlier, significant coolings could have also inferred cause a drastic reduction in the temperature of the summer months, the length of the growth season resulting in a transformation of the flora and the fauna of the basin as well. Taxa characteristic of alpine cold steppes and the tundra turn up and become dominant in the northern part of the basin bringing about a retreat of open parklands hosting spruce, Scots pine and scattered deciduous elements locally and regionally.

The dominant taxa of the arboreal vegetation are Swiss pine *(Pinus cembra),* juniper *(Juniperus)* and larch *(Larix).* However, the proportion of arboreal elements and woodlands was highly reduced surviving only in sheltered refugees of the basin (WILLIS et al., 2000). The dominant elements of the flora during these times were heliophyllic non-arboreal plants including artemisia *(Artemisia),* grasses *(Gramineae)* and members of the orpine family *(Crassulaceae).* At the same time several cold-loving tundra elements like stone-breakers *(Saxifraga)* and other perennial elements (*Androsace*) also turn up. A dominance of a treeless steppe vegetation could be postulated mixed with perennial elements and scattered trees. Thus despite the emergence of a dominantly loess steppe environment in the northern areas of the Carpathian Basin, the mosaic development of environmental parameters enabled the sporadic survival of a forest-steppe vegetation with an extremely low proportion of arboreal elements as well.

During the most prominent coolings, the cold-resistant and cold-loving elements turned up in the

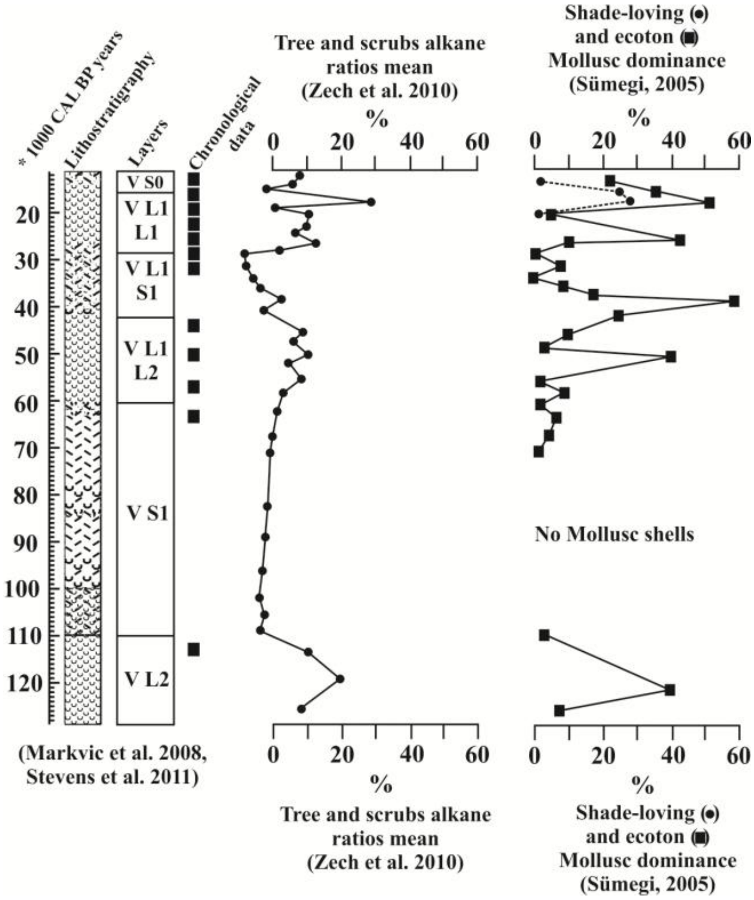

Fig. 2b. Changes observed in the composition of plant alkanes and the terrestrial mollusk fauna in the area of the Southern Great Hungarian Plains for the past 130 kys

2b. ábra. A növényi alkánok és a Mollusca fauna összetételének változása az elmúlt 130 ezer évben a Dél-Alföldön

V S0 = Vojvodina, modern soil, V L1L1 = Late Pleniglacial Loess layer, V L1S1 = Middle Pleniglacial Paleosol layer, V L1L2 = Early Pleniglacial Paleosol layer, V S1 = Last Interglacial and Early Weichselian Paleosol layers, V L2 = Saalian Loess layer

V S0 = Vajdaság, recens talaj, V L1L1 = késő-pleniglaciális lösz, V L1S1 = középső-pleniglaciális paleotalaj, V L1L2 = kora-pleniglaciális paleotalaj, V S1 = utolsó interglaciális talajréteg, V L2 = Riss löszréteg southern parts of the Carpathian Basin parallel with a gradual retreat of warmth-loving Southeastern European mollusk elements, including the character elements of the Pannonian forest-steppe. The analysis of mollusk faunas dated to the LGM in profiles from the Southern Great Hungarian Plains yielded surprising results. Here the expansion of cold-loving tundraic elements *(Columella columella, Vallonia tenuilabris)* was accompanied by the spread of Central European woodland elements *(Clausilia dubia, Clausilia pumila, Cochlodina laminata, Macrogastra ventricosa, Aegopinella ressmanni, Discus ruderatus, Orcula dolium)* (SÜMEGI, 2005; HUPUCZI – SÜMEGI, 2010). On the basis of these findings we may postulate only a slight decrease in the temperature for areas located at lower latitudes during the LGM. At the same time this decrease in the temperature resulted in a significant rise in relative humidity favoring the spread of arboreal elements (trees, bushes). The general composition of the mollusk fauna indicates the emergence of a forest steppe vegetation in the southern parts of the Carpathian Basin during the LGM, extremely rich in species and with a dominance of cold-resistant and eurytopic species.

Based on our results a relatively stable woodland-grassland ecotone with fluctuating proportion of arboreal elements and taxa was the dominant vegetation type of the Carpathian Basin between ca. 140 and 16 kys. This ecotone, as show by the paleoecological record was by no means uniform, but a multiple mosaic patterning is presumed observable on local, regional and basin wide scale as well. The emergence of macro or basin-scale mosaic patterning was attributable to the interplay of climatic influences, including the rainshadow effect of the basin and the actual distance from the continental and alpine ice cover. As a result the presence of two distinct paleoenvironmental, paleobiogeographical units covering an area of ca. 50–100 thousand km^2 could be postulated for the ice age of the Carpathian Basin. One of these entailed the northern areas, while the other the southern areas of the basin. Regional and local differences in the bedrock geology, soils, geomorphology and hydrology further dissected these two major units to smaller mosaic components at a scale of some hundred or some km^2. This multiple mosaic patterning of the paleoenvironment attributable to climatic, orographical, geological and hydrological endowments was the most important of feature of the Carpathian Basin enabling the collective presence and survival of floral and faunal elements sometimes with contrasting ecological needs. It was this mosaic patterning of the paleoenvironment which enabled the long-term sustainment of a woodland-grassland ecotone in the basin within the course of fluctuating climatic evolution of the ice age. Furthermore, the presence of multiple ecological habitats also ensured the survival of cold-resistant taxa during the warmings and warmths-loving taxa during the coolings in specially sheltered habitats. This phenomenon is known as the dual refugee effect in the literature (WILLIS et al., 1995). The general structure of a woodland-grassland ecotone was preserved even during the largest coolings, during phases of a treeless steppe. However, locally there must have been some homogenization of the vegetation in the northern parts and plant mosaics must have been preserved in shelters of favorable microclimate, along the watercourses or on slopes, walls, valleys with a southern exposure (WILLIS et al., 2000).

Paleoenvironmental development during the Pleistocene/Holocene transition

The first emergence of the Pannonian forest steppe, corresponding to the westernmost isolated part of the Eastern European forest-steppe belt, is generally dated to the opening of the Holocene (bw. ca. 10–8.5 kys cal BP); i.e. the Boreal in the literature (JÁRAINÉ-KOMLÓDI, 2000; ZÓLYOMI – FEKETE, 1994). According to this concept, the emergence of an extremely dry climate during the referred period must have triggered the opening of the mixed taiga hosted by the area of the Great Hungarian Plains due to specific edaphic factors enhancing the invasion of heliophyl steppe and Pontic elements into the initial clearings and the retreat of pine to the higher, cooler areas and cold-spots of the basin. This hypothesis considers the opening of a mixed taiga as the main trigger in the formation of a temperate forest steppe during the initial part of the Holocene. Conversely, as it was stated in the previous chapter, the emergence of a stable forest steppe could have been attested even during the ice age as well on the basis of paleoecological data. Furthermore, representatives of the Southeast European warmth-loving mollusk *Granaria frumentum*, which is also a character element of the modern Pannonian forest-steppe were present during this period in the southern parts of the basin and managed to survive even the largest coolings (SÜMEGI – KROLOPP, 2002). So on the basis of our findings, the most important elements of the forest-steppe within a mosaic setting were present preceding the Holocene as well. The appearance of warm steppe, forest-steppe elements in the pollen spectrum could have been correlated with the intrusion of warmth-loving, steppe/forest-steppe dweller mollusks in the loess profiles of the Southern Great Hungarian Plains dated between 16–15 kys cal BP and including the character species of the Pannonian forest-steppe Granaria frumentum. Based on the paleorecords, a woodland-grassland ecotone emerged in areas of higher and lower groundwater table of the plains. The dominant elements were those of temperate steppe in areas of lower groundwater table with a subordinate presence of trees. Conversely, areas with more favorable hydrologies hosted a mixed taiga studded by grassland spots of *Artemisia* steppe. So according to these records, the immigration of warmth-loving floral and faunal elements responsible for the creation and sustainment of a modern temperate forest-steppe in the basin must have initiated as early as 16/15 kys cal BP in the southern parts of the Carpathian Basin. However, the local and regional climate, morphology, hydrology and geology have significantly influenced the trajectory of evolution. Nevertheless, one must also bear in mind the potential influences of ice age megaherbovires of the so-called mammoth steppes in the sustainment of a woodland-grassland ecotone (GUTHRIE, 2001; ZAZULA et al., 2002, 2003, 2007). The presence of mammoth, wild horses, reindeer, moose and buffalos could have been univocally attested in the study area for the referred period (KRETZOI, 1977; JÁNOSSY, 1979; VÖRÖS, 1987; KORDOS, 1987; PAZONYI 2004). The general composition of this Upper Würmian mammal fauna also indicates a species-rich forest-steppe vegetation in the area of the Carpathian Basin (SÜMEGI, 2005) as numerous woodland elements (moose, reindeer) were collectively present with typical steppe dwellers (GUTHRIE, 2001). Furthermore, these herds of megaherbivores must have significantly contributed to the reduction of arboreal vegetation in the area. The notion of a forest-steppe is corroborated by data on rodents (KORDOS, 1987) and birds, where typical steppe or tundra elements like the great bustard *(Otis tarda)*, or ptarmigan *(Lagopus lagopus, Lagopus mutus)* are complemented by typical woodland elements like various taxa of woodpeckers *(Caprimulgus europaeus, Dendrocopos major, D. medius, D. leucotos, Picus canus, Jynx torquilla)* in sites dated to the terminal part of the last ice age (JÁNOSSY, 1979). Thus besides the referred edaphic and climatic factors, the new steppe/forest-steppe grazers and rodents must have contributed to the sustainment of a Subcontinental- Submediterranean oak forest-steppe of the Early Holocene of the Carpathian Basin (SÜMEGI, 2005).

Paleoenvironmental development during the Early Holocene

There is a marked transformation between 11,5 and 9,5 kys cal. BP.. The proportion of pine pollen grains goes below 10% here giving way to the advent of thermomesophilous trees and bushes including oak, lime, elm, hornbeam and alder. The high concentration of flue ash within this horizon marks the outbreak of natural fires in elevated temperatures. No wonder the ratio of AP:NAP was reduced to 50% in this horizon. Thus according to the paleorecord, the environmental changes dated to the Pleistocene/Holocene transition favored the spread of woodlands (mixed taiga exchanged by deciduous woodlands) in the marginal foothills of the Carpathians as well as the hilly and mid-mountain regions of the basin. At the same time the heart of the basin witnessed the emergence of a temperate forest-steppe. According to the data available, the intrusion of thermo-mesophilous trees and steppe elements occurred within a mesophilous mixed forest-steppe vegetation after the LGM between 16–15 kys cal BP. Then increasing temperatures and a rise in natural fires contributed to the disapperance of cold-resistant elements and the emergence of a Subcontinental-Submediterranean oak forest steppe. Based on investigation results a marked local and regional decrease in relative humidity could have been inferred during the opening of the Holocene parallel with increasing temperatures. This might have favored the general reduction of woodlands, expansion of grasslands and thus the sustainment of temperate forest-steppes during the Holocene in the area of the Great Hungarian Plains. All in all, paleoenvironmental changes preceding the Holocene transition must have favored the intrusion and expansion of thermo-mesophilous elements from their refugees found in the southern parts of the Carpathian Basin into a mosaic of boreal type forest-steppe, which had emerged in the terminal ice age. By ousting the previously dominant cold-resistant and mesophilous taxa, they must have contributed to the gradual emergence of a temperate oak forest steppe in the Carpathian Basin even preceding the actual boundary of Pleistocene/Holocene. Natural fires set in a woodland of easily flammable pines must have significantly accelerated the development of forest-steppes. A very similar vegetation change leading to the emergence of a Subcontinental-Submediterranean oak forest-steppe was modeled for the area of the Eastern European Plains based on paleobotanical records (NOVENKO et al., 2011). However, as shown by the chronology, this type of transformation must have occurred much earlier in the area of the Carpathian Basin, probably as a result of heightened drop of humidity attributable to the basin effect related to increasing temperatures, plus the relative vicinity of refugees of the warmth-loving, steppe elements aiding quick colonization (WILLIS et al., 1995, 2000). A characteristic feature of the Carpathian Basin is that the extant megaherbivores of the ice age were replaced woodland elements like roe-deer, deer, auroch, wild boar. At the same time in sites of the Great Hungarian Plains remains of typical steppe elements like wild horse *(Equus ferus)* and onager *(Equus hemionus)* turn up in large numbers (VÖRÖS, 1987). The presence of wild horse could have been attested from 62, while that of onager from 21 Holocene sites in Hungary (VÖRÖS, 1987). Remains of steppe dweller wild ass *(Asinus hydruntinus)* have also been retreieved from various archeological sites of the Great Hungarian Plains dated between 7000–11000 years (BÖKÖNYI, 1992). This latter taxon went extinct ca. 6–7 kys ago, but the presence of wild horse and onager could have been traced as far as the Bronze Age (3000–3500 BC). Domesticates replacing these wild forms and other grazers (caprines, cattle, horses, pigs) have also ensured the sustainment of a forest-steppe, steppe environment in the basin. The collective presence of new woodland elements and steppe/forest-steppe elements of the wild fauna is another independent proof of the mosaic patterning of the Holocene forest-steppe vegetation of the Great Hungarian Plains well before the emergence of first agricultural groups. A similar duality is seen in the record of early Holocene rodent remains. Woodland elements are complemented by typical steppe/forest-steppe elements like birch mouse *(Sicista),* mole rat *(Spalax),* gopher *(Citellus citellus),* hamster *(Cricetus cricetus).* The early Holocene avifauna of the Great Hungarian Plains is likewise dominated by steppe/forest-steppe elements including the Great bastard *(Otis tarda),* the Blacktail Godwilt *(Limosa limosa)* in same proportions as other woodland elements. Thus besides the referred edaphic and climatic factors, the new steppe/forest-steppe grazers and rodents must have contributed to the sustainment of a Subcontinental-Submediterranean oak forest-steppe of the Early Holocene of the Carpathian Basin.

Paleoenvironmental development from the settlement of the first farmers

The first farming groups, connected to the early Neolithic Körös culture turn up in the Holocene Subcontinental-Submediterranean oak forest-steppe of the Great Hungarian Plains roughly 8000 years ago. Many researchers blamed these first farming groups for the initial human-induced vegetation changes. However, recent paleoecological and paleoenvironmental studies of Mesolithic and Neolithic cultures of the Carpathian Basin and the Great Hungarian Plains yielded surprising results. In the horizon of woodland profiles dated to the Late Mesolithic a clear, iterative signal of vegetation changes could have been identified seen in periodic increases in flue ash, the appearance of open area taxa and the cyclical reduction of elm and hazelnut pollen concentrations. These changes were interpreted as the side-effects of human activities related to the creation of seasonal hunting camps and paths, intensive foraging and the use of twigs and leaves as fodder favoring the expansion of open areas in closed woodlands and the spread of heliophyl marginal vegetation. Conversely, no such changes could have been identified in the horizons of catchments of small lacustrine basins and marshlands from the heart of the basin (Great Hungarian Plains) found next to Early Neolithic sites and dated to the Late Mesolithic and Early Neolithic. Furthermore, besides an obvious increase in cereal pollen grains, no other signs of vegetation disturbance related to agricultural activities could have been attested. Despite their extensive settlement of more than 3000 sites identified, no clear sign of fire-induced deforestation by members of the Early Neolithic Körös culture could have been proven in the heart of the basin. Conversely, results of phytolith and mollusk analysis implemented on material from the Early Neolithic sites themselves have corroborated the presence of extensive grassy spots and arable lands in the direct vicinity of the sites. Representatives of the Körös culture chose to settle on the floodplain of the Tisza River and its tributaries. These settlements however were not confined to the actual riverbed but were placed on top of the flood-free, loess-covered island like lag-surfaces at an interface of multiple ecotones as shown by the findings of detailed geoarcheological investigations implemented in the vicinity of Körös sites in Hungary. These island-like lag surfaces were covered by chernozem soils, which developed on the loessy bedrock, hosting a steppe/forest-steppe vegetation. The sites thus were located at the interface of the higher floodplain hosting a steppe/forest-steppe and the adjacent low floodplain hosting a hardwood gallery forest. This mosaic of multiple ecotones ensured the engagement of multifocal subsistence on the one hand.

On the other hand, thanks to the relative openness of the natural highs hosting the settlement there was no need of deforestation for the creation of living space and arable/or pasturelands. This is a highly intriguing example of how the mosaic-like multiple ecotone of woodland-grassland areas influenced settlement and subsistence strategies of first farming groups of the Great Hungarian Plains. It is interesting to note though that numerous even more extensive steppe-forest steppe areas are found several kms away from the rivers like those of the Hortobágy and the Hajdúság (SÜMEGI, 2005) yet they were colonized during the second half of the Neolithic only. All in all based on our data, the continuous presence of a forest-steppe nestled in the heart of the Carpathian Basin made human disturbances obsolete for ensuring economic activities of the first farming groups. Sings of human disturbances could have been attested in the marginal areas of the basin, where the natural development of the landscape favored the sustainment of closed woodland and did not result in the emergence of forest-steppe areas. Vegetation changes related to conscious human intervention in the landscape like burning, the expansion of weeds and the reduction of the arboreal vegetation in a forest-steppe environment are traceable from the Late Neolithic and Early Copper Age. Five such stages were differentiated from the Late Neolithic, Early Copper Age. Stage one is hallmarked by the settlement of the Late Copper Age Badenian and the Pit Grave Cultures. Settlement was so extensive that human influences were attested in alkaline areas of the Great Hungarian Plains as well. Stage two is put to the Middle Bronze Age and the emergence of multilayered (tell) settlements hallmarking the height of preurban societal evolution in the area. The vicinity of these tell settlements were intensively exploited hallmarked by such activities as the establishment of floodplain orchards (walnut production), a complete transformation of hardwood gallery forests. The extremely focused exploitation of the landscape during the establishment of the tell settlements brought about a complete disappearance of the boundaries between closed woodlands and adjacent forest-steppe areas contributing to the expansion of the ecotonal elements to the former areas of gallery forests and the closed woodlands of the hills and foothills as well as mid-mountains of the basin. Signs of deforestation are most pronounced in fortified tell sites, where the creation of palisades required large amounts of timber.

The continuation of human disturbances characteristic of the Middle Bronze Age is postulated for the Late Bronze Age and the Early Iron Age as well. However, the focus of human activities was displaced from the area of the original, natural forest-steppes to those of natural woodlands in Transdanubia and the Subcarpathian region. Around the newly established fortified military centers, located in a woodland setting a full transformation of the landscape and the vegetation is discernible yielding the emergence of wide open areas. These transformations favored the intrusion of non-arboreal elements indigenous of adjacent natural forest-steppes as well as that of weeds. The resulting woodland-grassland ecotone in a natural woodland setting was the clear outcome of human activities here dated to the Late Bronze and Early Iron Ages. Signs of extensive deforestation during the referred periods are recorded in the catchment basins, hallmarking intensive soil erosion and inwash and contributing to the paludification and silting up of minor creek beds, ponds under the Early Iron Age rainfall maximum. The littoral region of larger lakes and the banks of larger rivers were silted up to such an extent, that a clear advent of reed, bulrush and sedge was traceable there.

The next stage is connected to the invasion of Celtic tribes conquering the entire basin and in possession of high-tech iron tools. Human-induced forest-steppe development could have been attested along numerous settlement points. Based on the analysis of plant remains retrieved from Celtic features a clear transformation of the agricultural activities can be postulated. A drastic drop in the areas under woodland cover is likewise discernible parallel with the expansion of arable lands, orchards and pasturelands becoming the focus of economic activities during the Late Iron and the Imperial Ages. Thus these Celtic tribes were engaged in extensive plant cultivation, high-class gardening and animal husbandry. The strong presence of wine grapes and chestnut in the array of plants cultivated by the Celts is outstanding in our understanding of the emergence of Submediterranean agriculture of the Imperial Age as it clearly shows the local roots of such activities. The highly intertwined agricultural activities of the Late Iron Age and Imperial Age reach such heights in the area of the Carpathian Basin, that they are even recorded in the diaries of imperial travelers as well dated to the 3rd 4t^{h} centuries AD. Other hallmarks of intensive human activities include the well-constructed and maintained network of roads and the defense line of the limes. The transformation of the floodplain of the Danube valley during the reign of the Roman emperors reached such heights that it brought about a complete disappearance of the natural woodlands on the side of Pannonia province. When counter-fortresses were constructed on the other side of the Danube, it also resulted in the disappearance of the natural woodland there as well. The creation of artificial steppes accompanying the construction of roads and defense systems favored the colonization of the species to these areas as well.

It must be noted here that although human-induced transformations of the landscape are largely recorded in the Transdanubian side of the Pannonia province for the referred period, changes were likewise large-scale on the other side of the basin populated by barbarian herds. Sarmatian tribes characterized by extensive animal husbandry and high population numbers and later adopting Roman type economic activities had similarly large impact on the landscape of the Great Hungarian Plains. Incipient wind-blown sand movements in areas under an original forest-steppe cover are perhaps the best markers of intensified landscape exploitation (KISS et al., 2006). Overgrazing of sandy steppes, forest-steppes by members of a group characterized by nomadic pastoralism was an important trigger of anthropogenic sand movement. These changes however by no means were unique. Similar negative outcome could have been attested to tribes settling the area during the Migration Age, including the nomadic Avars and the Hungarians as well. Cumanians settling the area before and after the Mongolian invasion caused similar landscape changes in the wind-blown sandy areas of the Great Hungarian Plains (SÜMEGI, 2001; KISS et al., 2006). The pastoral practices of these nomadic tribes, when complemented by dry spells of the climate resulted in the creation of semi-desert environment in certain parts. These were counterbalanced by periods of higher rainfall and the transformation of agricultural practices to avoid the full degradation of the landscape yielding a forest-steppe again in the long run. Nevertheless, these highly degraded landscapes have also pointed to the high vulnerability of this unique ecosystem. Although these transformations clearly highlighted periods, when the limit of sustainability was reached no truly irreversible transformations can be inferred in the landscape until the 19th century. The period of the Middle Ages, although characterized by intensive human activities, favored the preservation of mosaic-patterning present in the vegetation thanks to the array of productive techniques adopted ensuring the collective presence of meadows, pasturelands, cultivated arable lands, fallows, remnant natural and artificial woodlands. Thus the original structure of the forest-steppe ecotone and the most important composing taxa was more or less preserved. The appearance of Turkish rule and the desertification of certain urban areas of the Great Hungarian Plains further enhanced the natural regeneration of the Pannonian forest-steppe and these conditions prevailed up to the second half of the 17th century. It was the time when maize (Turkish wheat in original name) was first introduced via Turkish means to the area of the Great Hungarian Plains. This crop altered the way people thought about animal husbandry and resulted in the introduction of intensive stall-feeding where corn gave the main fodder. The introduction of this new line of thinking fundamentally transformed the way landscape was treated. The traditional system of meadows-pasturelands and arable lands was abandoned and there was a huge hunger for the exploitation of new lands to provide higher yields. This could have been achieved by the drainage of waterlogged areas, peatlands and the plowing of meadows and pasturelands alone. The lack of male labor force as an outcome of the Napoleon wars resulting in extremely high wheat prices was a further push factor to achieve these goals in hope of a greater profit putting the owners of the agrarian system to the side of river regulations and the acquisition of new land for production. The complete destruction of the original structure and composition of the Pannonian forest-steppe is attributable to the 19th century flood protection and river regulation measures seen in the creation of vast dike and canal systems and the drainage of the landscape to acquire new land suitable for intensive cereal production. It was this time when the ecological foundation of the area was overthrown: the hydrology. As the natural supply of climate-induced loss of water of the landscape via floods ceased, the ecological systems whose functioning is based on the availability of water collapsed. Industrial agricultural production resulted a complete homogenization of the vegetation creating a so-called cultural landscape or better to say "cultural desert". This process is still active and the extreme droughts and increasing temperatures of the past 50 years favored the emergence of a steppe-like environment in the heart of the basin (PÁLFAI, 1989). A major deal is whether or not this process will halt at a certain point or will result in a complete degradation of the landscape. It's quite clear though that the natural system of multiple ecotones was seriously damaged and could be restored by special measures of experts working collectively for the restoration and conservation of the landscape.

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AZ ERDŐSSZTYEPP HOSSZÚ TÁVÚ FEJLŐDÉSE AZ ALFÖLDÖN PALEOÖKOLÓGIAI ADATOK ALAPJÁN

A Kárpát-medence centrumában egy a jégkor végi hidegmaximumot követően kialakult boreális erdőssztyepp szerkezetbe termomezofil fajok telepedtek meg 16 ezer cal BP évet követően. Ez a fajgazdag, tűlevelű erdőelemekkel jellemezhető boreális erdőssztyepp a jégkor végén, a holocén kezdetére átalakult és egy kontinentális–szubmediterrán elemeket tartalmazó erdőssztepp alakult ki a medence centrumában. Ezek a változások rendkívüli mértékben hasonlítanak a kelet-európai síkságon kifejlődött erdőssztyepp területeken kimutatható változásokhoz, de a Kárpát-medencében ezek a folyamatok korábban játszódtak le. Ugyanakkor a medencében, a terület geográfiai pozíciója következtében erőteljesebb óceáni és szubmediterrán, sőt a hegykoszorú következtében szubkárpáti éghajlati hatás is kifejlődött, szemben a Kelet-Európai Síksággal. Az éghajlati hatások, az éghajlati határfelületi helyzet nyomán a pontusi, balkáni, atlanti, valamint hegyvidéki elemek jelentkeznek a kontinentális erdőssztyepp elemek mellett a medencében. Vagyis az éghajlati határfelület mellett a vegetáció határfelülete is kialakult. Az erdőssztyepp környezetet kialakító éghajlati hatások közül a legjelentősebb a nyári félév hőmérséklete, csapadékösszeg és a nyári félévnek a párolgási tényezői és ezekkel összefüggésben lévő relatív nedvesség emelhető ki, mert ezek a tényezők teljes mértékben átfedőek az alföldi erdőssztyepp határával. A medence centrumában kialakult erdőssztyeppet a hegységi, dombsági és magasabb térszíni, jelentősebb csapadékbevétellel jellemezhető területeken zárt lomboserdő vette körül. A Holdridge féle bioklimatológiai osztályozás alapján az alföldi erdőssztyepp a hidegmérsékelt füves puszta – a hidegmérsékelt üde erdő és a melegmérsékelt száraz erdő közötti átmeneti (ökoton) zónában alakult ki, ahol az átmeneti régióban a melegmérséklet szárazerdő – a hidegmérsékelt füves puszta és a hidegmérsékelt üde erdőfoltok és sávok egyaránt megtalálhatók egy mozaikos szerkezetet alkotva.

Az éghajlati hatások mellett a Kárpát-medencében a holocén kezdetére kialakult erdőssztyepp fejlődésére az edafikus (domborzati, geológiai, hidrológiai és talajtani) adottságok is hatással voltak. Ezek a folyamatok legjobban a már a jégkor végétől kifejlődött speciális talajvízforgalomhoz, kőzet – talajvíz – talaj – növényzet kapcsolatokhoz köthető szikes területeken követhetők nyomon. A holocén kezdetére kialakult mérsékeltövi erdőssztyepp kifejlődésében, stabilizációjában a természetes tüzek, döntően lágyszárúakat fogyasztó nagytestű növényevők csordái, a tömegesen jelentkező, sztyeppei környezetet igénylő rágcsálók is jelentős szerepet játszottak. A kora holocén halász – vadász – gyűjtögető mezolit kultúrák és a neolit közösségek ebben a mozaikos szerkezetű, erdőfoltokból, sztyeppfoltokból és átmeneti (ökoton) sávokból álló fajgazdag környezetben éltek. Mivel megtelepedési pontjaik ezeknek a kultúráknak elsősorban a nyitottabb növényzeti foltokhoz kötődött ezeknek a közösségeknek számottevő módon nem alakították át az erdőssztyepp szerkezetét, bár a neolit közösségek növénytermesztésük révén új fajokkal, köztük gyomokkal gazdagították az erdőssztyepp növényzetét és fenntartották az erdőssztyepp mozaikos, ökoton jellegét. Ugyanakkor ezek a közösségek az erdőssztyepp zóna peremén lévő, illetve a zónán belül hidegmérsékelt üde erdőkre már jelentősebb hatással voltak és tevékenységük nyomán a heliofil szegélyvegetáció terjedt ki ezeken a területeken. Az adatok alapján a jégkor végén kifejlődött mozaikos szerkezetű, ökoton jellegű erdőssztyeppek makroklimatikus, edafikus okok és a mezolitikumtól kezdődően az emberi hatások egyaránt szerepet játszottak a holocén kori stabilizációjában és fejlődésében. A késő neolitikumtól, rézkortól a háziasított legelő állatok jelentős állomány-növekedésének vagyunk tanúi, a gyomok terjedése szintén az emberi hatások kiterjedését jelzi, és a dombvidéki szántók is a középső újkőkor végén, valószínűleg jelentős népességnövekedés hatására terjedtek ki. Ezt követően a bronzkor közepétől, megközelítőleg az Kr.e. 1500 évtől történt egy újabb jelentős változás, a nagy testű növényevő fajok vad alakjai, talán a túlzott vadászat és domesztikáció nyomán, szinte nyomtalanul eltűntek a vizsgált térségből. Viszont a tenyésztett állatok csordái pótolták a vad alakok mozaikos növényzeti struktúrát fenntartó hatásait (rágás, taposás).

A jelentős népességszám-növekedés, a fejlettebb társadalmi berendezkedés, a több száz éven keresztül folyamatosan lakott stabil településeket kialakító bronzkori preurbánus fejlődés, a lakott térségeket, legelő- és szántóterületeket égetéssel kialakító, egyre jelentősebb tenyésztett állatállománnyal rendelkező közösségek hatására igen sok helyen a természetes fejlődés megszakadt, kultúrsztyeppék és kezelt erdők alakultak ki. Az emberi hatással zavart növényzeti foltok aránya a fémkultúrák kialakulásával, terjedésével fokozatosan növekedett és a bronzkor végére, a vaskor kezdetére az eredetileg teljesen erdősült területekre is kiterjedt olyan mértékben, hogy ezeken a területeken is növényzeti ökotonok, emberi hatás alatt álló erdőssztyeppék alakultak ki. Ezek a hatások a késő-vaskorban és a császárkorban még tovább erősödtek és szinte az egész medence antropogén hatású erdőssztyeppé alakult át. Az ókori, a népvándorlás kori és a középkori emberi hatások közül kiemelkedik a Kelet-Európai Síkságról a medencébe vándorolt nagyállattartó közösségek szerepe, mert a szárazabb éghajlati szakaszokban a megnövekedett állatállomány következtében helyenként túllegeltetés és ennek nyomán antropogén sztyeppei – félsivatagi környezet és futóhomokmozgás alakult ki. A mezőgazdasági szerkezeti váltások és a csapadékosabb szakaszok hatására ezek a növényzeti sebhelyek viszonylag gyorsan regenerálódtak és középkor végén, az újkor kezdetén a tradicionális, mozaikos környezetet fenntartó agrárközösségek révén a pannon erdőssztyepp szerkezete és fajkészlete szinte változatlanul fennmaradt. Sajnos az újkorban megjelent istállózó állattartás, a kukoricán hízlalásra áttérés és az ártéri legelők, rétek feltörése, majd a folyószabályozás nyomán kialakult kiterjed nagytáblás szántóföldi művelés nyomán a pannon ökoton növényzet szerkezete és szinte minden eleme végveszélybe került. Csak a XX. században, szinte az utolsó pillanatban létrehozott szigorú természetvédelmi intézkedések és a természetvédelmi szakemberek önfeláldozó munkája révén sikerült megőrizni és a túlfejlesztett mezőgazdasági területek revitalizálásával, erdőssztyepp növények és a természetes átmeneti ökoszisztémát stabilizáló állatok (vadlovak) újratelepítésével helyenként visszaállítani ezt a vegetációt. A pannon erdőssztyepp ökoton jellegű növényzet fennmaradás ennek ellenére kétséges a medencében, mert egyrészt a globális felmelegedés nyomán kialakuló szárazság okozta vegetációs változások, másrészt az összességében igen kis területre vonatkozó védelem, a fragmentáció, és a kiterjedt emberi tevékenység következtében rendkívül sérülékeny, megszűnés határán lévő állapotban van jelenleg.